

P. 6118

ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

December 1995

Volume 13, N° 3

Alytes, 1995, 13 (3): 81-86.

Bibliothèque Centrale Muséum

81



3 3001 00111594 7

Can anuran tadpoles choose among foods that vary in quality?

Cindy L. TAYLOR *, Ronald ALTIG ** & Carolyn R. BOYLE ***

* Department of Biology, Austin Peay State University, Clarksville, TN 37044, U.S.A.

** Department of Biological Sciences, Mississippi State University, Mississippi State, MS 39762, U.S.A.

*** Research Program, College of Veterinary Medicine, Mississippi State University, Mississippi State, MS 39762, U.S.A.

In feeding choice tests, tadpoles of *Rana sphenoccephala* and *Bufo woodhousii* chose agar-bound foods that contained catfish (protein 32.0, fat 5.0, fiber 12.0 %) over rabbit chow (18.0, 2.5 and 17.0 %) and foods bound in 0.5 vs. 1.0 % agar. *Rana* tadpoles did not distinguish between foods with X and 2X amounts of food per volume. Whether these choices were influenced by nutritional gain or other feeding stimuli is not known, but the data show that tadpoles do not feed indiscriminately.

INTRODUCTION

The amount of data available on the interspecific differences in selective suspension-feeding by tadpoles with (e.g., VIERTEL, 1990, *Bufo bufo* and *Rana temporaria*) and without (e.g., WASSERSUG, 1972, *Xenopus laevis*) keratinized mouth parts contrasts sharply with what is known about harvesting abilities of rasping tadpoles. Details of tadpole nutrition (e.g., MODZELEWSKI & CULLEY, 1974), which ingested materials are actually digested and assimilated, and the nutritional content and physical characteristics that may influence harvestability of natural foods, are poorly known. Even the designations of herbivores or detritivores can be challenged, and the few feeding studies present conflicting evidence of feeding selectivity. Dietary latitude surely is large in most circumstances, and differences in oral morphology presumed to influence feeding may only come into play during specific circumstances of community structure and food scarcity. Feeding interactions often are suggested in studies of interspecific competition, but the responsible mechanisms cannot be determined because we know so little about the mechanics of the oral structures and



the physical characteristics and microdistributions of food sources. Interspecific and ontogenetic physiological and enzymatic differences, which are seldom considered, may be important. STEINWASCHER & TRAVIS (1983) correlated the lack of effect of protein:carbohydrate ratio on tadpoles of *Rana sphenocephala* vs. better growth of *Hyla chrysoscelis* at a high ratio with the higher levels of proteases relative to amylases found in hybrid compared to ranid tadpoles (ALTIG et al., 1975).

As initial tests of interspecific differences in feeding of two lentic, benthic tadpoles that commonly co-occur, we asked if tadpoles can detect and choose between food sources that vary in three parameters of quality.

MATERIALS AND METHODS

Eggs of *Rana sphenocephala* were reared outdoors in plastic pools until groups were tested at total lengths (mm) of ca. 26 (stage 25, GOSNER, 1960), 35 (28) and 52 (33). Tadpoles of *Bufo woodhousii* (total length ca. 21 mm, stage 33) were collected from the field. Although differing in many details of their oral morphology, both of these benthic tadpoles have labial tooth row formulas of 2/3.

Two tanks with 10 or 12 equal, non-connected units (11 × 15 cm) provided 9 experimental and 1 or 3 control units per test. Groups of tadpoles (*Rana*, 10/unit; *Bufo*, 20/unit) and controls (no tadpoles) were assigned randomly to units during 3 replications of 10-12 groups; tadpoles were not fed for 24 h before a test. Groups of tadpoles were required to stimulate normal feeding behavior, and feeding times varied between species and sizes within a species (*Rana*) in order to realize sufficient removal to measure accurately (i.e., *Rana* at smaller sizes and one-half the number of tadpoles ate more than *Bufo*). We emphasize that only the choices made and the total amount of food removed in these preference tests were of interest and not the rate of removal.

A glass Petri dish divided into four 13.2 cm² quadrants was oriented arbitrarily near the center of each unit, and each quadrant contained 5 ml of a food bound in agar. Previous studies (JOHNSTON, 1982) showed that tadpoles readily eat this food, and natural foods of rasping tadpoles cannot be presented or recovered accurately. In Experiment I, each quadrant contained one of the following combinations: 0.2 g of pulverized Arko catfish chow (Attala Company, Kosciusko, MS; protein 32.0, fat 5.0, fiber 12.0 %) or Purina rabbit chow (18.0, 2.5 and 17.0 %) suspended in 0.5 or 1% agar. In Experiment II, opposite quadrants contained either 0.1 or 0.2 g of catfish chow suspended in 0.5 % agar. Food in like quadrants and controls within each test was derived from the same batch. Remaining food scraped into weighed dishes and dried for 12 h at 40°C was weighed (± 0.1 mg). The amount eaten was calculated by subtracting the dry weight of remaining food in each quadrant from the mean dry weight of the proper quadrants of controls. Tadpoles will switch between rasping and filtering modes of feeding dependent on the amounts of solid vs. particulate food present (STEINWASCHER, 1979). In this study, tadpoles were forced to feed by rasping because suspended particles were absent.

Percentages of food removed were arc-sine transformed for analysis. *Bufo* (binder concentration and food type) in Experiment I and *Rana* (tadpole size and food quantity)

in Experiment II were analyzed with a 2×2 factorial design in completely randomized blocks (PROC GLM, SAS INSTITUTE, 1988). *Rana* (tadpole size, food quantity and binder concentration) in Experiment I was analyzed with a $3 \times 2 \times 2$ factorial design in completely randomized blocks. Means that were significant were separated by the Least Significant Difference, the significance level was set at $P < 0.05$, and data are presented as means \pm S.E.

RESULTS

In Experiment I, tadpoles of *Bufo woodhousii* removed significantly more material from 0.5% than from 1.0%. The interaction of tadpole size \times binder density was significant for *Rana sphenoccephala* (Tables I and II). More of the 1.0% material was removed by medium-sized tadpoles than by any other combination of size class and binder density (Table II). The amount removed by large- and medium-sized tadpoles feeding on 0.5% agar ranked second in greatest amount removed, and small tadpoles feeding on 0.5% agar removed the least. Food containing catfish chow was eaten more readily than rabbit pellets by all sizes of tadpoles (Tables I and II).

In Experiment II, it appeared as if tadpoles of *R. sphenoccephala* removed significantly more material from quadrants with 0.2 g of food (58.1 ± 2.6 mg) than from quadrants with 0.1 g (28.5 ± 1.0 mg; see below), but this probably was not true (see below). Medium-sized tadpoles removed significantly more material than small or large tadpoles (Tables I and II).

DISCUSSION

Detection, choice and acquisition are required for successful feeding. Our data indicate that choices are made, but the fact that all quadrants were fed upon to some degree suggests sampling was required, even if a portion of the difference was caused by aggressive individuals pushing others into adjacent quadrants. Sampling suggests that taste or an evaluation of harvestability were involved; feeding stimulation by specific amino acids varies among herbivores (e.g., JOHNSEN & ADAMS, 1986) and carnivores (MACKIE, 1982), but there are no data on the chemical stimulants for tadpoles; social facilitation of feeding is known (ALTIG & CHRISTENSEN, 1981). Olfaction surely is important in finding a patch but apparently does not provide an evaluation of quality. If random encounter coupled with an inability to detect differences and/or a lack of motivation to move to a new patch was not present, feeding from the quadrants likely would not have been different. Time-course observations, to include diel patterns of feeding (e.g., WARKENTIN, 1992) will clarify some of the above questions.

Differences in the ability to harvest substrates of different densities imply quantitative interspecific differences in the mechanics of the feeding structures which likely translate to dietary latitude. Using 1% agar as the food binder, JOHNSTON (1982) found that the

Table I. - Summary of two- and three-way analysis of variance of amount of food-agar mixture removed by tadpoles of *Bufo woodhousii* and *Rana sphenoccephala* with respect to tadpole size, binder density and food type and quantity.

Source	df	SS	MS	F	P
<i>Bufo woodhousii</i> - Experiment I					
Food type	1	0.0001	0.0001	0.4	0.5569
Binder density	1	0.0013	0.0013	7.8	0.0068
Food x Bd	1	0	0	<0.1	0.9176
Error	67	0.0108	0.0002		
<i>Rana sphenoccephala</i> - Experiment I					
Tadpole size	2	0.0776	0.0388	58.7	0.0001
Food type	1	0.0053	0.0053	8.1	0.0048
Binder density	1	0	0	<0.1	0.9392
Ft x Bd	1	0.0003	0.0003	0.4	0.5374
Ts x Ft	2	0.0002	0.0001	0.2	0.8459
Ts x Bd	2	0.0119	0.0060	9.0	0.0002
Ts x Ft x Bd	2	0.0003	0.0001	0.2	0.8272
Error	312	0.2062	0.0007		
<i>Rana sphenoccephala</i> - Experiment II					
Tadpole size	2	937.5	468.7	4.6	0.0111
Food quantity	1	573.6	573.6	5.6	0.0187
Ts x Fq	2	150.0	75.0	0.7	0.4823
Error	308	31592.3	102.6		

Table II. - Mean amounts of food removed (mg) in Experiments I and II. Values are total amounts of food removed with no suggestion of rate of removal. Means not followed by the same letter are significantly different ($P = 0.05$). Tadpole size: S = small, M = medium and L = large; food type or quantity: CC = catfish chow, RP = rabbit chow; binder density: 0.5 or 1.0 % agar. Hyphen = factors not considered in a given test (see Table I).

Tadpole	Food	Binder	Eaten
<i>Bufo woodhousii</i> - Experiment I			
-	-	1.0	11.8 ± 1.8 b
-	-	0.5	20.2 ± 2.5 a
<i>Rana sphenoccephala</i> - Experiment I			
S	-	0.5	27.5 ± 1.9 d
-	-	1.0	30.0 ± 3.0 d
M	-	0.5	59.3 ± 3.6 b
-	-	1.0	72.4 ± 4.1 a
L	-	0.5	62.2 ± 4.6 b
-	-	1.0	46.0 ± 3.3 c
-	CC	-	53.6 a
-	RP	-	45.5 b
<i>Rana sphenoccephala</i> - Experiment II			
S	-	-	31.4 b
M	-	-	37.2 a
L	-	-	31.0 b
-	CC/0.1 g	-	28.5 b
-	CC/0.2 g	-	58.2 a

feeding marks made by *B. woodhousii* tadpoles showed that they have difficulty penetrating the substrate, while tadpoles of *Rana catesbeiana* and *Rana clamitans* of the same size fed readily. In our study, tadpoles of *B. woodhousii* removed 1.6 times as much 0.5 % as 1 % agar, and small tadpoles of *R. sphenoccephala* removed 2.5 times as much 1 % agar as similar-sized tadpoles of *B. woodhousii* regardless of the food content. Even large tadpoles of *R. sphenoccephala* chose the less dense binder when given a choice.

Because the material with 0.2 g of food weighed twice per volume of that with 0.1 g, we dismiss the statistical difference between the amounts that tadpoles of *R. sphenoccephala* consumed (28.5 vs. 58.2; Table II). That is, the tadpoles removed the same volume but twice the weight. Actual calories gained would have been larger in the food with 0.2 g of food, but the tadpoles did not distinguish between that food and the one with one-half the amount of food per volume. This contention cannot be resolved without knowing the number of bites taken, but it seems most likely that the tadpoles took the same number of bites from each one without distinguishing between nutrient densities. The interaction of tadpole size and binder density ($P = 0.0002$) was much stronger than tadpole size ($P = 0.0111$) and food type ($P = 0.0048$) alone. Two additional modifiers come to mind: would the tadpoles distinguish between these two foods if they were (1) presented throughout tadpole ontogeny or (2) physically separated so that energy expended in search times would have increased the demand for higher gains? The finding by STEINWASCHER (1979) that food concentration in agar pellets (no choice available) did not affect growth suggests that the lower concentration was adequate or that the tadpoles ate more of it.

Tadpoles approaching metamorphosis stop feeding as the mouth parts and gut start to atrophy at about stage 41, but more subtle ontogenetic changes in behavior associated with development are suspected. The tadpoles in these experiments were not approaching metamorphosis, so the discordance of amount eaten among sizes of tadpoles is of note; large tadpoles of *R. sphenoccephala* did not remove as much material as did medium-sized tadpoles. Ontogenetic differences in activity levels (LAWLER, 1989), physical interference among larger individuals around the dishes, and ontogenetic changes in the effectiveness of the digestive (WASSERSUG, 1975) or feeding apparatus are probable factors.

Epiphytic organisms *sensu lato* probably are much more important as food sources for tadpoles than either macroalgae or macrophytic plants to which they are attached (e.g., KUPFERBERG, MARKS & POWER, 1994), and presence of predators cause changes in foraging behavior (e.g., SEMLITSCH & REYER, 1992). In our study, tadpoles were presented with four adjacent choices and predators were absent, so exploration was minimal and with no predatory risk so that exploitation could be maximized. Under these circumstances, tadpoles can sample food sources, evaluate their quality and respond accordingly. The diet and feeding behaviors of tadpoles require a lot of research, but categorizing tadpoles as non-selective foragers appears unwarranted. We suggest that examinations of gut contents and particularly fecal examinations (e.g., PAVIGNANO, 1989) present inaccurate assessments of materials assimilated by tadpoles; at the moment we have no ideas on the relationships between that which is swallowed and that which is digested and assimilated. The materials that can be counted and identified likely have little to do with tadpole nutrition.

LITERATURE CITED

- ALTIG, R. & CHRISTENSEN, M. T., 1981. — Behavioral characteristics of the tadpoles of *Rana heckscheri*. *J. Herpet.*, **15**: 151-154.
- ALTIG, R., KELLY, J. P., WELLS, M. & PHILLIPS, J., 1975. — Digestive enzymes of seven species of anuran tadpoles. *Herpetologica*, **31**: 104-108.
- GOSNER, K. L., 1960. — A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, **16**: 183-190.
- JOHNSON, P. B. & ADAMS, M. A., 1986. — Chemical feeding stimulants for the herbivorous fish, *Tilapia zillii*. *Comp. Biochem. Physiol.*, **83A**: 109-112.
- JOHNSTON, G. F., 1982. — Functions of the keratinized oral features in anuran tadpoles with an analysis of ecomorphological tadpole types. Thesis, Mississippi St. Univ., Mississippi State: 1-43.
- KUPFERBERG, S. J., MARKS, J. C. & POWER, M. E., 1994. — Effects of variation in natural algal and detrital diets on larval anuran (*Hyla regilla*) life history traits. *Copeia*, **1994**: 446-457.
- LAWLER, S. P., 1989. — Behavioural responses to predators and predation risk in four species of larval anurans. *Anim. Behav.*, **38**: 1039-1047.
- MACKIE, A. M., 1982. — Identification of the gustatory feeding stimulants. In: T. J. HARA (ed.), *Chemoreception in fishes*, New York, Elsevier Press: 275-291.
- MODZELEWSKI, E. H., Jr. & CULLEY, D. D., Jr., 1974. — Growth responses of the bullfrog, *Rana catesbeiana*, fed various live foods. *Herpetologica*, **30**: 396-405.
- PAVIGNANO, I., 1989. — Method employed to study the diet of anuran amphibians larvae. *Amphibia-Reptilia*, **10**: 453-456.
- SAS INSTITUTE, Inc., 1988. — *SAS/STAT User's guide*. Release 6.03 ed., Cary, NC, SAS Institute Inc.
- SEMLITSCH, R. D. & REYER, H.-U., 1992. — Modification of anti-predator behaviour in tadpoles by environmental conditioning. *J. anim. Ecol.*, **61**: 353-360.
- STEINWASCHER, K., 1979. — Competitive interactions among tadpoles: responses to resource level. *Ecology*, **60**: 1172-1183.
- STEINWASCHER, K. & TRAVIS, J., 1983. — Influence of food quality and quantity on early larval growth of two anurans. *Copeia*, **1983**: 238-242.
- VIETEL, B., 1990. — Suspension feeding of anuran larvae at low concentrations of *Chlorella* algae (Amphibia, Anura). *Oecologia*, **85**: 167-177.
- WARKENTIN, K. M., 1992. — Microhabitat use and feeding rate variation in green frog tadpoles (*Rana clamitans*). *Copeia*, **1992**: 731-740.
- WASSERSUG, R., 1972. — The mechanism of ultraplanktonic entrapment in anuran larvae. *J. Morphol.*, **137**: 279-288.
- 1975. — The adaptive significance of the tadpole stage with comments on the maintenance of complex life cycles in anurans. *Am. Zool.*, **15**: 405-417.

Corresponding editor: Günter GOLLMANN.